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Symmetry breaking in cyclic competition by niche construction

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ABSTRACT

Niche construction theory, which portrays organisms as active agents that modify their environment rather than mere passive entities selected by their environment, has received increasing attention in ecology and evolutionary biology. Here, we investigate the ecological consequences of niche construction in the system of three cyclically competing metapopulations, engaging a rock–scissors–paper game. Using cellular automata, we detected a variety of dynamic behaviors, including damped oscillation, periodical fluctuation and stage equilibrium, and the system transformed from disorder to order with gradually increasing niche-constructing intensity. Increasing niche-constructing intensity of a species, counterintuitively, reduced its own occupancy, but increased that of its inferior competitor. These species displayed interesting ripples in the two-dimension lattice space, with the pattern sensitive to the symmetry of competition intensity and other vital rates. Spatial heterogeneity induced by niche construction, together with the competition hierarchy, formed a stable and fixed range for each species with clear boundaries. Our results highlighted the necessity of investigating the adaptive dynamics of niche constructing traits to better understand the eco-evolutionary consequence of niche construction.

1. Introduction

Niche construction, where organisms can actively modify their environment rather than being passively selected by the environment, is a recent concept in evolutionary ecology [1–5]. It refers to the capacity of organisms to construct, modify, and select important components of their environment to meet their niche demand, such as through building nests and burrows, releasing chemicals and nutrients, which consequently modify both abiotic and biotic forces of natural selection in the local environment. In doing so, niche construction could generate a feedback between environmental processes and eco-evolutionary ones [4,6–10]. Niche construction could, arguably, be an evolutionary process by its own right, rather than a mere product of evolution [11–13]. Nonetheless, niche construction can be considered equivalent to ecosystem engineering at the ecological time scale, often through modifying the flow of energy and matters in ecosystems [2,3,14].

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To date, the majority of theoretical models for describing the dynamics of niche construction have confirmed that niche construction can remarkably affect the dynamics and distribution of involved species [2,3,8–10,15,16]. For example, Hui et al. [15] found that organism-environmental feedbacks from niche construction can profoundly affect the outcome of competition and the maintenance of biodiversity in metapopulations, mainly through forming self-organized environmental heterogeneity and range-limited species distributions. Han and Zhang [16] expanded on Tilman's multi-species competition model by incorporating niche construction component to illustrate that niche construction also affects the ecological order of metapopulation, i.e. the sequence of populations' occupy proportion of habitat. In a model of two consumers that compete for one limiting resource but consumed by one common predator, niche construction can either generate net interspecific facilitation or strengthen interspecific competition via altering the balance between intraspecific and interspecific competitive effects [3]. Through rescuing the depleting resource, niche construction can also foster species coexistence [3]. Various processes of niche construction can also lead to diverse spatial distributions of species such as spiral wave, spiral-broken wave and circular wave [9], and it can even restrain gene flows along environmental gradients via forming fitness valleys [10].

Cyclic population dynamics, as manifested in the rock–scissors–paper game, have been previously studied by many for elucidating the mechanisms of biodiversity and self-organized patterns using lattice models and partial differential equations (e.g., [17–38]). Results from most these models show the emergence of self-organized spatial distribution of species and complex patterns of coexistence, such as entangled rotating spiral waves (e.g. [17,18,22–24,35,38]), remarkable target-wave [25,38], chaotic patches [26] and phase transition of suddenly appearing large-scale fluctuations [20,36]. These various outcomes can be explained by the topological shape, spatial structure, interaction range and rate, as well as species (or player) numbers in the ecological or evolutionary network [30]. Reichenbach et al. [23] have analyzed the spiral waves from low mobility and computed the wavelength and spreading velocity of spirals. Evidently, biodiversity in a community experiencing cyclic competition depends heavily on the difference between species' mobility (or invasion rate) [26,30]. Protection spillovers where species A indirectly facilitates species B via suppressing the natural enemies of B, may also change the dynamics of cyclic dominance fundamentally in structured populations, which could underpin the phenomenon of microbial coexistence [38]. A recent study on the population dynamics of three cyclically competing species in a two-dimensional turbulent fluid system sheds new insight to how turbulent transportation affects ecosystem structure in communities without a clear competition hierarchy [32]. It has also been widely observed in cyclic game models of the dominance of inferior species (e.g., [17–19]). Studies on an extension of the rock–paper–scissors game, named the finger game [27] or rock–paper–scissors–lizard–Spock (RPSLS) game [29,36] which includes five species along a cyclic hierarchy, also confirmed that a large number of species and high mobility can jeopardize biodiversity maintenance and potentially lead to diverging fluctuations under strong mixing [36]. In a six-species predator–prey cyclic system, an unexpected non-monotonous dependence of alliance survival on special heterogeneous invasion rates, even with the Gaussian noise, was revealed [33,34]. The extinction time of a well-mixed four cyclically competing species was estimated to have correlated linearly with the system size, and the probability distribution of extinction time takes roughly the shape of a shifted exponential distribution [28,31]. Szolnoki et al. [37] showed that the transition from pairwise to group interactions can decelerate or even reverse the direction of invasion between competing players. Time-dependent factors were also found important for cyclic system; different capacities of learning by players in the spatial prisoner's dilemma game offer alternative ways for the persistence of cooperators [35].

Cyclic competition can also emerge spontaneously in evolutionary public goods games with volunteers [39], peer punishment [40], pool punishment [41,42], reward [43,44] and reciprocity [45]. A spatial public goods game generally includes three elementary strategies: to defect, to reward and to punish. Other deformations of this classic setup have resulted in rich dynamic behaviors [41,42,45]. For example, defection remains viable when the rewarding is costly. Moderate rewards may promote cooperation better than big rewards, especially if the return from cooperative contributions is low [44]. Moreover, regardless of the return ratio which governs the public goods game, punishment in particular are more effective in deterring defection than the combined strategy of punishment, reward or defection [45]. Indeed, this topic has received a comprehensive review recently (see [30]).

Symmetry, meaning uniformity or invariance in patterns or structures, is often appealing and inspiring in natural systems [46]. Symmetry breaking is the process by which the uniformity is broken so to generate a more structured and improbable state in the focal system [47]. In general, increasing levels of broken symmetry in systems are often associated with increasing complexity and functional specialization of system components [46], and are true in biology across all system scales, from the macromolecules https://en.wikipedia.org/wiki/Symmetry_breaking_and_cortical_rotation-cite_note-3 to tissues and organs (see [48–55]). In ecological systems, symmetry breaking has received wide attention especially under the framework of cyclic competition, partly because the asymmetric scenarios can be diverse. For instance, if the dispersal rates of all species are close/similar to each other, the coexistence takes the form of spiral waves or target waves [22]. The spiral dynamics, however, do not appear if the species have unequal mobility. The greater the disparity between dispersal rates, the shorter the distance to the origin at which the spiral waves break down, and the dynamics begin to resemble several tangled spirals, eventually without forming spirals [26,27]. In systems of marine phytoplankton [56] and atmospheric microbes [57], advection and diffusive transportation in cyclic competition can further interact with the environment and form a complex interplay of diverse factors dictating symmetry breaking [32].

Here, we investigate the ecological consequences of niche construction in three cyclically competing species. Competition among these three species resembles the game of rock–scissors–paper (as in Zhang et al. [58]). The rock species R can invade the habitat patches occupied by the scissors species S; the scissors species S can invade the habitat patches occupied

by the paper species P; and the paper species P can invade the habitat patches occupied by the rock species R. There are a number of natural systems resembling our model setup, such as coral reef invertebrates [59], lizards in the inner coast range of California [60] and microbial populations of colicinogenic *E. coli* [61]. Based on the cyclic-competition model, we further allow the three species, through niche construction, to modify their own habitat resources and constrain the accessibility of resources of other species. By comparing the spatiotemporal dynamics from our model with those observed in Zhang et al. [58], we explore how niche construction affects the outcome and dynamics of cyclic competition, and how it interferes the effect of inter-species differences in vital rates on the emerged spatial patterns.

2. Model

Tilman's multi-species model of competing metapopulations assumes that all species are arranged in a simple competitive hierarchy, ranking species from the best competitor to the worst [62]. Superior competitors can invade habitat patches occupied by inferior competitors and displace them instantaneously, whilst inferior competitors cannot displace species of higher competitive hierarchies. Based on this competition model, Zhang et al. [58] constructed the following model for the rock (species 1), scissors (species 2) and paper (species 3) species engaging cyclic competition:

$$\begin{aligned}
\frac{dP_1}{dt} &= c_1P_1(1-P_1-P_3)-e_1P_1-c_3P_3P_1,\\
\frac{dP_2}{dt} &= c_2P_2(1-P_2-P_1)-e_2P_2-c_1P_1P_2,\\
\frac{dP_3}{dt} &= c_3P_3(1-P_3-P_2)-e_3P_3-c_2P_2P_3
\end{aligned} \tag{1}$$

where P_k is the fraction of habitat patches occupied by species k $(=1,2,3)$; c_k and e_k $(c_k > e_k)$ are the colonization and extinction rate of species k, respectively.

We focus on examining the process of niche construction in these species. Let R_k be the resource type needed by species k. Following Laland et al. [1,63], we define positive niche construction as a process that can increase the resource content. Specifically, we assume that through niche construction process a species can increase the amount of its own resource and reduce the amount of resource on which its inferior competitor relies. Further considering the processes of resource recovery and dissipation, we have the following resource dynamics equations,

$$\begin{aligned}
\frac{dR_1}{dt} &= \alpha_1P_1-\alpha_3P_3-\gamma_1R_1+\varepsilon_1,\\
\frac{dR_2}{dt} &= \alpha_2P_2-\alpha_1P_1-\gamma_2R_2+\varepsilon_2,\\
\frac{\mathrm{d}R_3}{\mathrm{d}t} &= \alpha_3P_3-\alpha_2P_2-\gamma_3R_3+\varepsilon_3
\end{aligned} \tag{2}$$

where α_k, γ_k and ε_k $(k=1,2,3)$ are respectively the intensity of niche construction, the independent process of resource dissipation and recovery, satisfying the condition that α_k, γ_k and ε_k lie within the interval [0,1] and that $0 \le \alpha_k+\gamma_k+\varepsilon_k \le 1$. If there is no niche construction $(\alpha_k=0)$, the equilibrium of resource k is given by $R_{k0}=\varepsilon_k/\gamma_k$. For simplicity, we fix the values of $\gamma_k(=0.2)$ and $\varepsilon_k(=0.1)$ in the following analyses but only focus on the role of changing the intensity of niche construction.

The ability for effectively selecting feeding sites is a major determinant of species' survival, growth, and reproductive success. Some evidence indicates that cost-benefit relationships (e.g., resource availability and competition risks) may affect the behavior of animals [64,65]. Optimal foraging theory predicts that animals should forage for longer periods in high-quality patches than in poor-quality ones [66]. The spatial distribution of resources is particularly important for determining competition outcomes. To depict the effect of niche construction more intuitively, we define the colonization rate of a species as an increasing function with resource suitability. Using the simplest form of resource utilization spectrum, we assume that the optimum resource level of a species is equal to the equilibrium of resource level without niche construction, R_{k0}, and hence the resource suitability of each species can be defined as $\omega_k=\exp[-\lambda_k(R_k-R_{k0})^2]$, where $1/\lambda_k$ depicts the niche breadth of species k. In the following, we let $\lambda_k=3$. The colonization rate of species k is assumed to be proportional to the resource suitability, $c_k=c_{k0}\omega_k$, where c_{k0} $(k=1,2,3)$ is the maximum colonization rate. Furthermore, as there is only a limited amount of time and energy for growth, structure maintenance and reproduction, an organism must allocate its captured resources among these alternative needs [67]. To this end, we consider a simple trade-off between the maximum colonization rate and the ability of niche construction, $c_{k0}+\alpha_k=1$.

To investigate the spatial dynamics and pattern formation of niche-constructing metapopulations, we construct a cellular automaton in a 2D lattice arena with a number of $n\times n$ patches with synchronized updating, von Neumann neighbors and periodic boundaries. Simulations were implemented according to the probability transition model [68,69]. Assuming $P_{k,t}(i,j)$ indicates the probability that patch (i,j) is occupied by a local population of species k at time t, we have the following

probability transition rules:

$$P_{1,t+1}(i,j) = P_{1,t}(i,j) + \left[c_{10}\omega_{1,t}(i,j)\frac{\sum P_{1,t}(i,j)}{4}(1 - P_{1,t}(i,j) - P_{3,t}(i,j)) - e_1 P_{1,t}(i,j) \right] - c_{30}P_{3,t}(i,j)P_{1,t}(i,j)$$

$$P_{2,t+1}(i,j) = P_{2,t}(i,j) + \left[c_{20}\omega_{2,t}(i,j)\frac{\sum P_{2,t}(i,j)}{4}(1 - P_{1,t}(i,j) - P_{2,t}(i,j)) - e_2 P_{2,t}(i,j) \right] - c_{10}P_{1,t}(i,j)P_{2,t}(i,j)$$

$$P_{3,t+1}(i,j) = P_{3,t}(i,j) + \left[c_{30}\omega_{3,t}(i,j)\frac{\sum P_{3,t}(i,j)}{4}(1 - P_{2,t}(i,j) - P_{3,t}(i,j)) - e_3 P_{2,t}(i,j) \right] - c_{20}P_{2,t}(i,j)P_{3,t}(i,j)$$

where $\sum P_{k,t}(i,j)$ is the sum of the probabilities of species k in the four neighboring patches at time t. Correspondingly, the dynamics of different resources (only giving the case of R_2 for short) in patch (i,j) is given by:

$$R_{2,t+1}(i,j) = R_{2,t}(i,j) + [\alpha_2 P_{2,t}(i,j) - \alpha_1 P_{1,t}(i,j) - \gamma_2 R_{2,t}(i,j) + \varepsilon_2]$$

Note that we did not implement the possibility of resource diffusion between patches as it is normally much slower than the movement of individuals. Using the probability transition model, the spatial distribution patterns of cyclic competition can be explicitly revealed.

3. Results

Let us consider a simple case of symmetric (equal) vital rates among species ($c_k = c$, $\alpha_k = \alpha$ and $e_k = e$); that is, the three species are identical in their ecological properties except along a cyclic competition hierarchy. Setting the right side of Eq. (1) to zero, we can obtain a nontrivial equilibrium of the system:

$$P^* = (P_1^*, P_2^*, P_3^*) = \left(\frac{1 - \frac{e}{c}}{3}, \frac{1 - \frac{e}{c}}{3}, \frac{1 - \frac{e}{c}}{3} \right) \tag{3}$$

Because of $c + \alpha = 1$, the nontrivial equilibrium can also be expressed as $\frac{1}{3}(1 - \frac{e}{1-\alpha}, 1 - \frac{e}{1-\alpha}, 1 - \frac{e}{1-\alpha})$, which needs to satisfy the condition $\alpha + e < 1$ to ensure the metapopulation persistence.

For an asymmetrical structure that the three species are distinct in their colonization, extinction and niche constructing rates, more complicated equilibriums and various dynamical behaviors emerge. The non-trivial equilibrium of the metapopulations is as follows:

$$P_1^* = \frac{1 - \frac{e_1}{c_1} - \left(1 - \frac{e_3}{c_3}\right)l_3 + \left(1 - \frac{e_2}{c_2}\right)l_2 l_3}{1 + l_1 l_2 l_3}$$

$$P_2^* = \frac{1 - \frac{e_2}{c_2} - \left(1 - \frac{e_1}{c_1}\right)l_1 + \left(1 - \frac{e_3}{c_3}\right)l_3 l_1}{1 + l_1 l_2 l_3}$$

$$P_3^* = \frac{1 - \frac{e_3}{c_3} - \left(1 - \frac{e_2}{c_2}\right)l_2 + \left(1 - \frac{e_1}{c_1}\right)l_1 l_2}{1 + l_1 l_2 l_3}$$

where $l_1 = 1 + \frac{c_1}{c_2}$, $l_2 = 1 + \frac{c_2}{c_3}$, $l_3 = 1 + \frac{c_3}{c_1}$. The equilibrium of metapopulations not only depends on the original occupancy equilibrium $(1 - e_i/c_i)$, but also on the ratio of a species' colonization rate to that of its inferior competitor (l_i). Meanwhile, the equilibrium of resources is given as the following:

$$R_1^* = \frac{\varepsilon_1}{\gamma_1} + \frac{P_1^*\alpha_1 - P_3^*\alpha_3}{\gamma_1}$$

$$R_2^* = \frac{\varepsilon_2}{\gamma_2} + \frac{P_2^*\alpha_2 - P_1^*\alpha_1}{\gamma_2}$$

$$R_3^* = \frac{\varepsilon_3}{\gamma_3} + \frac{P_3^*\alpha_3 - P_2^*\alpha_2}{\gamma_3}$$

Clearly, the resource equilibrium is not only affected by the processes of resource dissipation and recovery, but also by the niche-constructing behavior, implying the importance of niche construction for the resource level and thus the resource suitability and persistence of each species.

When fixing parameters ε_k and γ_k, the system dynamics is mainly affected by the parameters of niche-constructing intensity (α_k) (thus also the colonization rate through the trade-off) and extinction rate (e_k) of species k $(= 1, 2, 3)$. We first observed the dynamical behaviors of the system using numerical simulations. Parameters were chosen to reflect the symmetry and various hierarchies of the system so that all possible outcomes can be embodied. From the diagrams of occupancy frequencies and trajectories in the phase space (shown in Fig. 1), three typical oscillatory dynamics were presented, including the stage equilibrium (Fig. 1a–d), the periodical oscillation of limit cycle (Fig. 1e and f), the damped oscillation (Fig. 1g–j). When the three species were symmetrical (identical in vital rates), the amplitude of their oscillatory dynamics increased synchronously and stayed at an equal level (Fig. 1a and b). However, this synchronized and identical dynamics

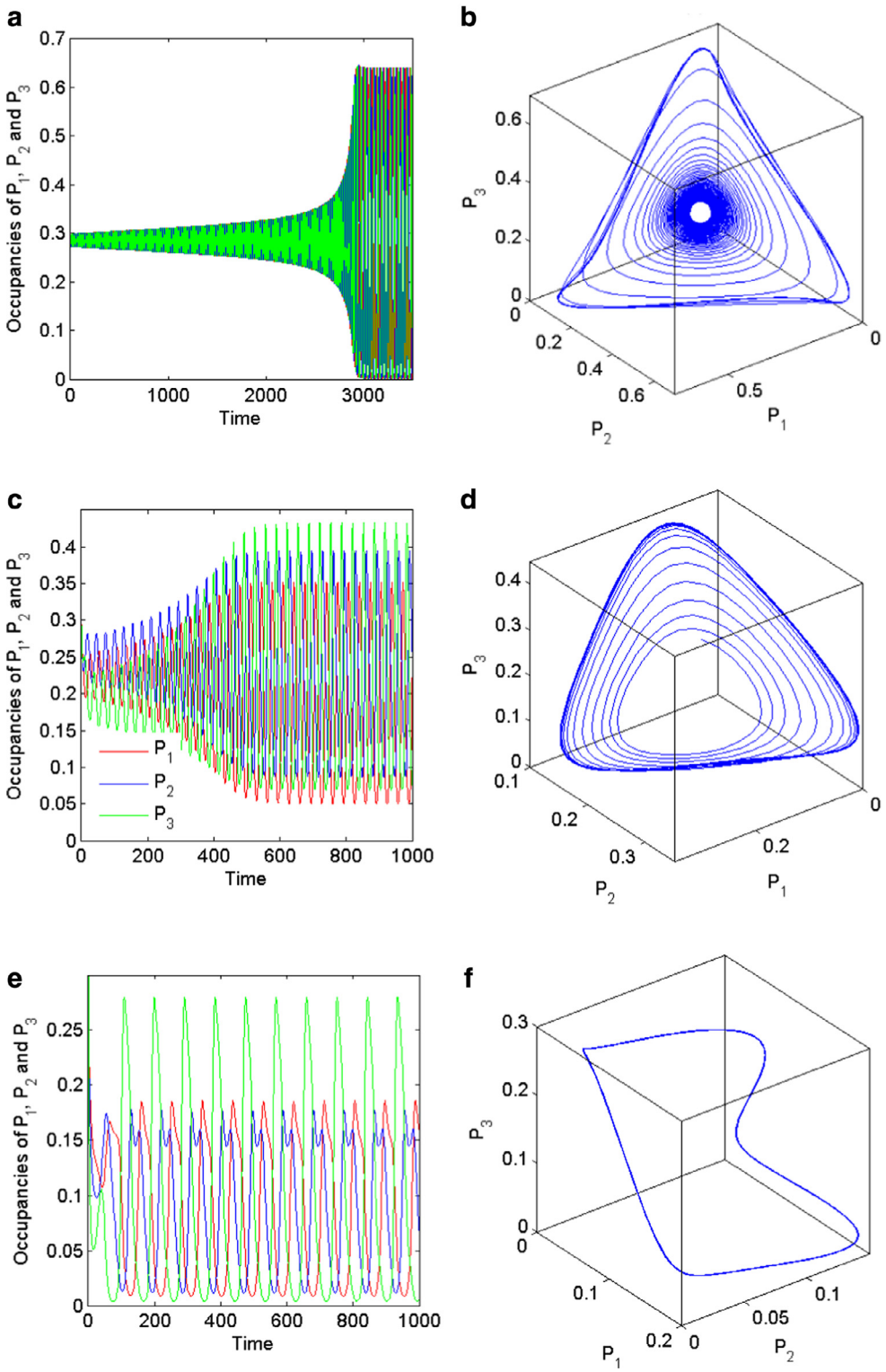

Fig. 1. Temporal dynamics and phase-plane portraits of occupancies of the three species. Parameters are (a) and (b) $\alpha_1 = \alpha_2 = \alpha_3 = 0.3$, $e_1 = e_2 = e_3 = 0.1$; (c) and (d) $\alpha_1 = 0.5$, $\alpha_2 = 0.4$, $\alpha_3 = 0.3$, $e_1 = 0.1$, $e_2 = e_3 = 0.2$; (e) and (f) $\alpha_1 = 0.7$, $\alpha_2 = 0.5$, $\alpha_3 = 0.2$, $e_1 = 0.1$, $e_2 = 0.3$, $e_3 = 0.5$; (g) and (h) $\alpha_1 = 0.5$, $\alpha_2 = 0.4$, $\alpha_3 = 0.4$, $e_1 = 0.1$, $e_2 = e_3 = 0.2$; (i) and (j) $\alpha_1 = \alpha_2 = \alpha_3 = 0.2$, $e_1 = 0.2$, $e_2 = 0.1$, $e_3 = 0.05$. The red, blue and green colors respectively refer to species P_1, P_2 and P_3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

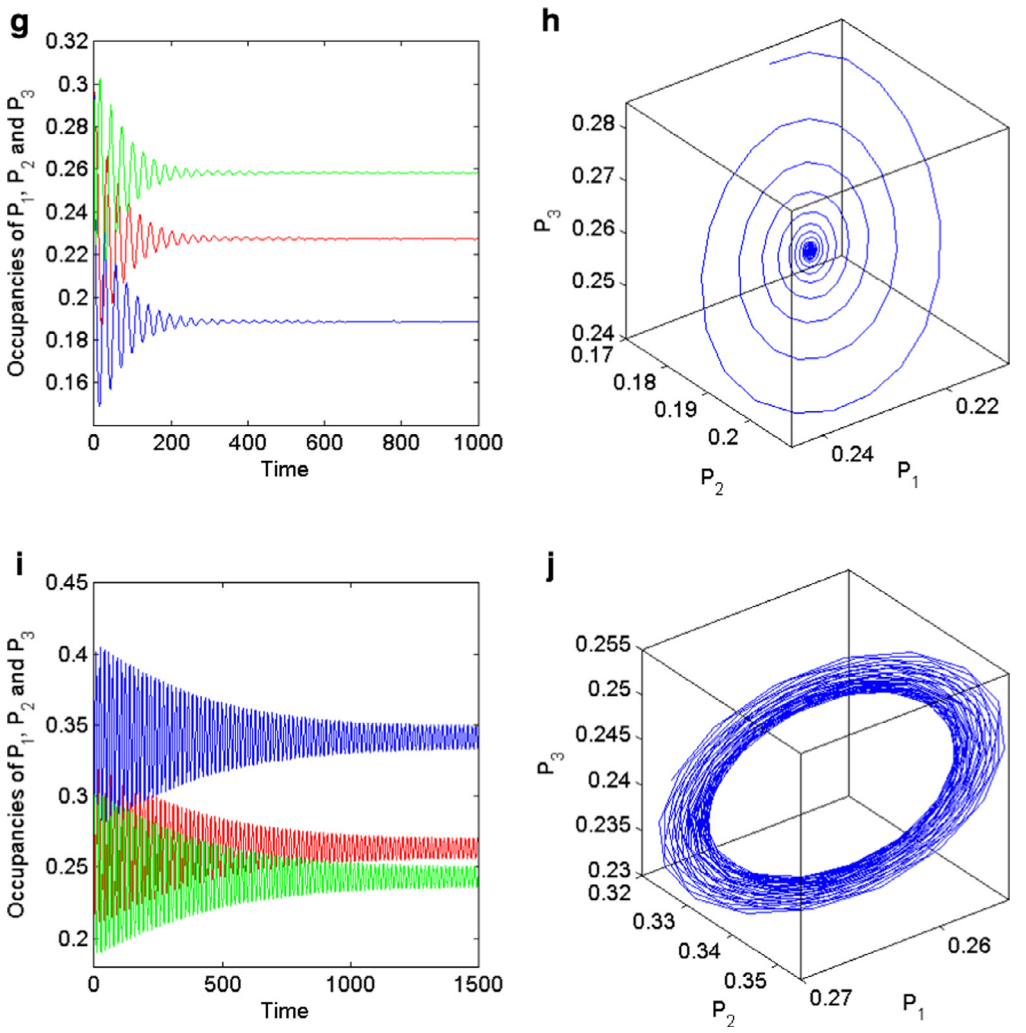

Fig. 1. Continued

broke once allowing differences in species' niche constructing intensity. Interestingly, high intensity of niche construction always led to a low level of occupancy (Fig. 1c and d). When the three niche-constructing intensities were set along a hierarchy ($\alpha_1 > \alpha_2 > \alpha_3$), the system exhibited the limit cycle (Fig. 1e and f). The above dynamics of the system are the typical, representing all possible behaviors in the cyclic networks, which have been referred to as oscillatory, absorbing and stationary phases (*sensu* [30]).

Bifurcation analysis was conducted to demonstrate the effect of changing niche-constructing intensity on metapopulation dynamics. Maximal conditional Lyapunov exponent was calculated for checking the system sensitivity to the initial values of state variables and whether chaos behavior exists. Fixing three extinction rates as $e_i = 0.1$ $(i = 1, 2, 3)$ and assuming that the niche-constructing intensities of species 1 and 3 are equal. As the increasing of $\alpha_1 (= \alpha_3)$, we examined how the changing niche-constructing intensity of species 2 affects system dynamics (Fig. 2). Two obvious features appeared when α_2 increases. First, the Lyapunov exponents of the system are $(0,\ 0,\ -)$ at the point of $\alpha_1 = \alpha_2 = \alpha_3$ and its neighborhood, which means the torus of system. When $\alpha_2 > 0.5$, the Lyapunov exponents are $(-,\ -,\ -)$. Here, species 1 was nearly extinct, and the system converged to a fixed point. Moreover, species 2 exhibited marked advantages in occupancy when $\alpha_2 < \alpha_1 = \alpha_3$, but gradually became the inferior when $\alpha_2 > \alpha_1 = \alpha_3$. Species 1 and 3, meanwhile, were converging to opposite directions, with species 3 eventually becoming dominated in number. This result suggests that the increase of niche-constructing intensity of a given species can counterintuitively decrease its own occupancy but increase the occupancy of its inferior competitor (Fig. 2a and c). The situation of $\alpha_1 = \alpha_2 = \alpha_3$ is an important turning point of system dynamics. The system transformed from disorder (Fig. 2b) to more orderly behavior (Fig. 2h) with gradually increasing niche-constructing intensities of species 1 and 3 ($\alpha_1 = \alpha_3$).

As asymmetrical conditions produced more complex behavior, we further examined the effects of inter-species difference on system behavior. Let $\alpha_1 = \alpha_2 - \delta$ and $\alpha_3 = \alpha_2 + \delta$, where δ is the parameter that describe inter-species difference in

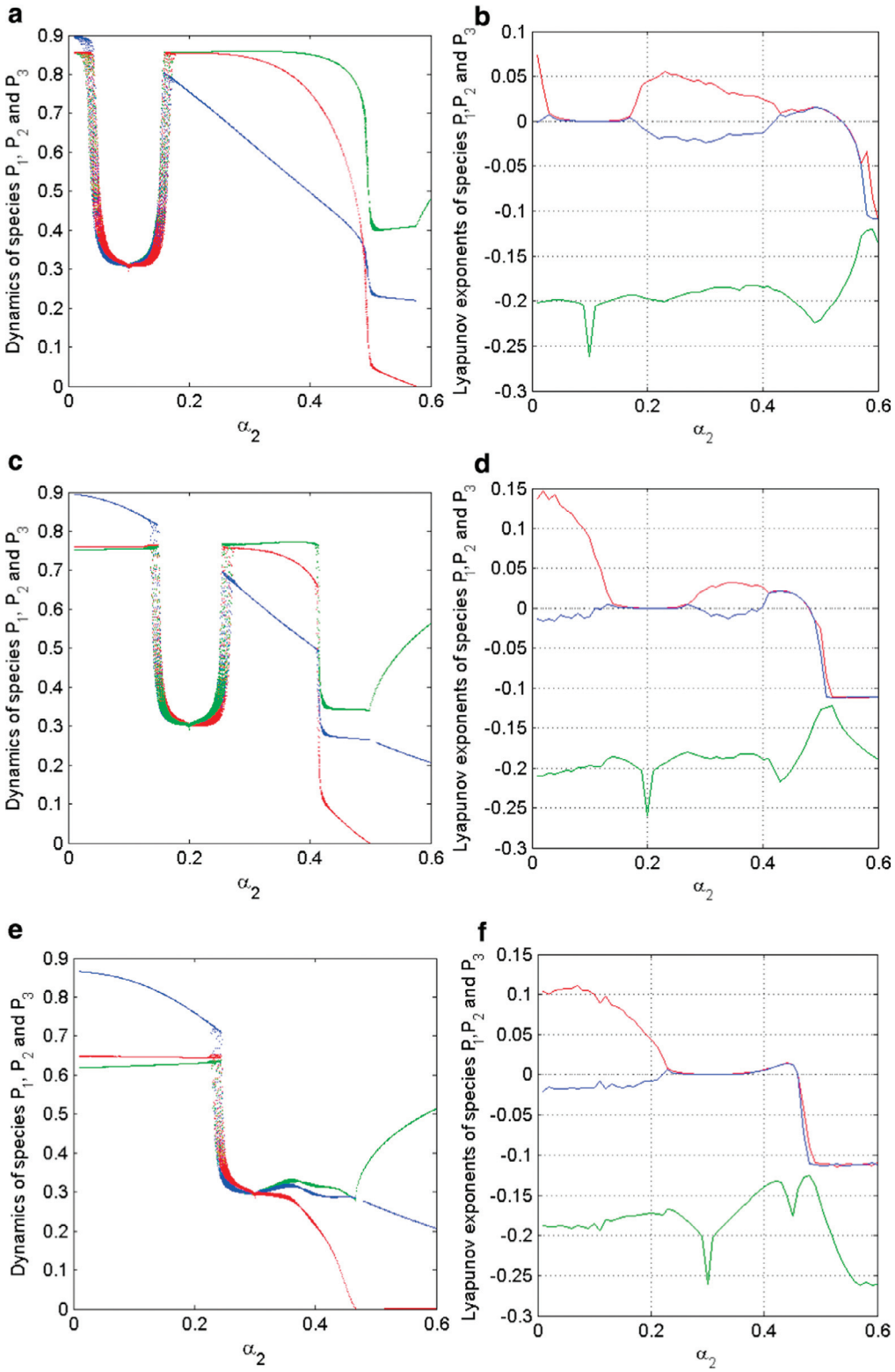

Fig. 2. The bifurcation diagram and corresponding Lyapunov exponents of three species as a function of increasing niche-constructing intensity. Parameters are $\alpha_1 = \alpha_3 = 0.1$ in (a) and (b); $\alpha_1 = \alpha_3 = 0.2$ in (c) and (d); $\alpha_1 = \alpha_3 = 0.3$ in (e) and (f); $\alpha_1 = \alpha_3 = 0.4$ in (g) and (h). The extinction rates are $e_1 = e_2 = e_3 = 0.1$. The red, blue and green lines represent the species 1, 2 and 3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

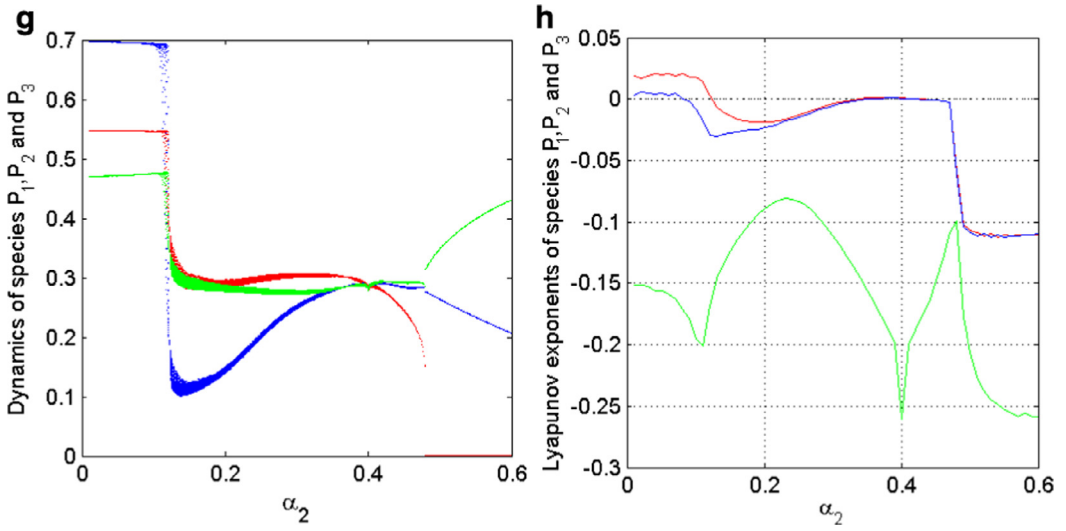

Fig. 2. Continued

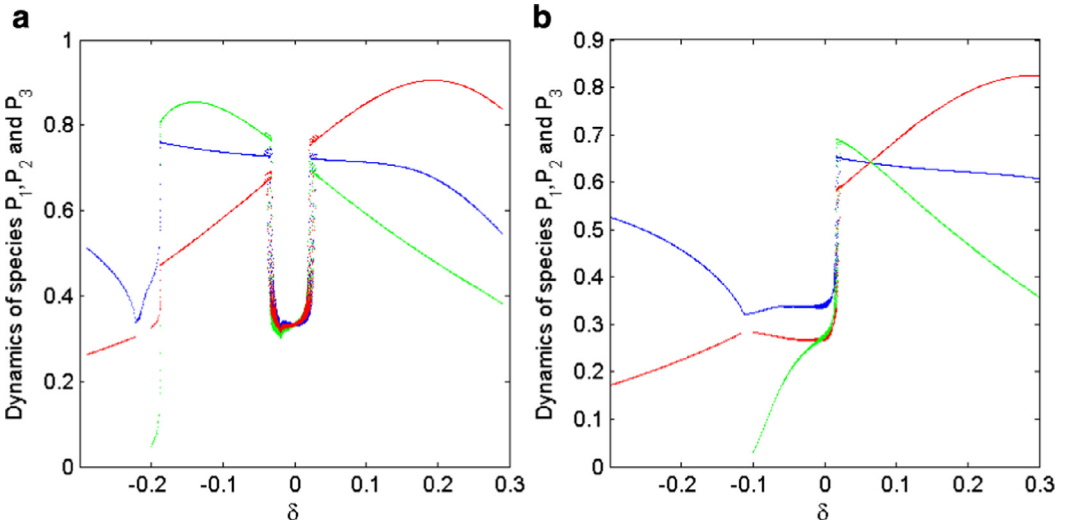

Fig. 3. The bifurcation diagrams of three species with increasing difference in niche-constructing intensities among species δ. We keep $\alpha_2 = 0.3$; (a) extinction rates of three species are equal: $e_1 = e_2 = e_3 = 0.05$; (b) extinction rates are: $e_1 = 0.15, e_2 = 0.1, e_3 = 0.05$. The red, blue and green lines represents the species 1, 2 and 3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

niche-constructing intensity. Fixing the value of parameter α_2, we thus have that, the larger parameter δ is, the greater the differences among species are. Moreover, the condition $\alpha_1 > \alpha_2 > \alpha_3$ is satisfied when $\delta < 0$, while $\alpha_1 \langle \alpha_2 < \alpha_3$ when $\delta \rangle 0$. Bifurcation diagrams of the three species influenced by δ were drawn (Fig. 3). Under the condition of equal extinction rates of the three species (Fig. 3a), the occupancies of these species moved in opposite directions with their niche-constructing intensities, excepting $\delta \in (-0.03,\ 0.03)$. More specifically, we have $P_1 < P_2 < P_3$ when $\delta \in (-0.2,\ -0.03)$, while $P_1 > P_2 > P_3$ when $\delta \in (0.03,\ 0.3)$. Moreover, the bigger the absolute value of parameter δ was, the more the difference of three species' occupancies were. For the situation of unequal extinction rates (Fig. 3b), the overall trend is similar to Fig. 3a. Although the extinction rate of species 3 was minimal, its survival range was the narrowest. When $\delta < -0.1$, species 3 almost definitely cannot survive. Species 2 had a bigger occupancy than species 1, suggesting that the species with a lower colonization rate and a higher extinction rate cannot reverse the disadvantage of situation, even if it has a stronger niche-constructing ability. When $\delta > 0$ (i.e. $\alpha_1 \langle \alpha_2 < \alpha_3,\ \ c_1 \rangle c_2 > c_3$, and setting $e_1 > e_2 > e_3$), the occupancy of species 1 and 3 respectively went straight up and then suddenly dropped, while that of species 2 remained at the same level. These results suggest that the role of niche construction is heightened in the cases of either minor differences of niche construction among species or small magnitude of the difference between colonization rate and extinction rate of species (e.g. the species 3 when $\delta = 0.3$). The ability of niche-construction cannot completely determine the fate of system, only partially playing the regulation role for cyclic competition. In addition, the threshold values leading to the extinction of species 3 were $\delta = -0.2$ in Fig. 3a and

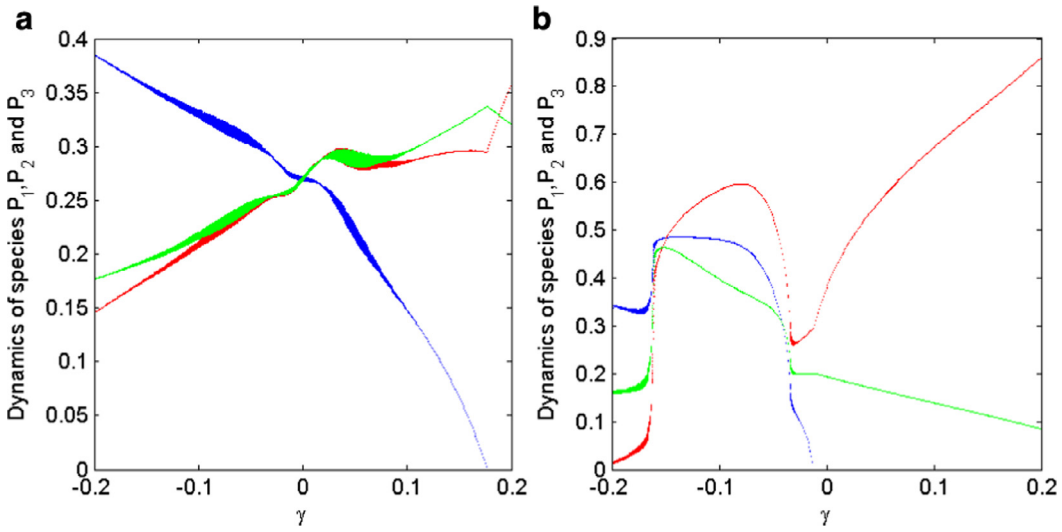

Fig. 4. The bifurcation diagrams of three species influenced by difference in extinction rate γ. We keep $e_2 = 0.2$, then $e_1 = e_2 - \gamma$, $e_3 = e_2 + \gamma$; the niche-constructing intensities are (a) $\alpha_1 = \alpha_2 = \alpha_3 = 0.2$; (b) $\alpha_1 = 0.1$, $\alpha_2 = 0.3, \alpha_3 = 0.5$. The red, blue and green lines represents the species 1, 2 and 3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$\delta = -0.1$ in Fig. 3b, respectively, because of the different initial values of three resources. It is also the reason of asymmetry showing between positive and negative parameters δ.

Species dynamics was also affected by their extinction rates. Considering the trade-off between niche construction and colonization and the necessary condition of persistence $c_k > e_k$, we assumed $\alpha_k + e_k < 1$ and selected two scenarios to discuss the effect of extinction rates on the dynamics of the three species. Also assume $e_1 = e_2 - \gamma$ and $e_3 = e_2 + \gamma$, where γ is the parameter describing extinction rate's difference. The bifurcation diagrams were shown in Fig. 4a ($\alpha_1 = \alpha_2 = \alpha_3 = 0.2$) and Fig. 4b ($\alpha_1 = 0.1$, $\alpha_2 = 0.3$, $\alpha_3 = 0.5$). Obviously, when there was no difference in species' niche-constructing intensities, the system dynamics was completely determined by extinction rates. With parameter γ increasing from negative to positive, the extinction rates of three species was gradually transformed from a descending trend to an increasing trend. During this change, the occupancy of species 2 sharply declined and even perished; in contrast occupancies of those other two species were rising steadily (Fig. 4a). In other words, the increase of extinction rate for a given species (species 3) can lead to the reduction of its superior competitor's occupancy, but counter-intuitively increase the occupancy of its own and its inferior competitor. Even if the extinction rate of species 3 was the highest, it may still have a high occupancy. This result suggests that the cyclic competitive structure of a system is a key factor to dictate the fates of the three species in case of equal niche-constructing intensities. The shape of the occupancy of these three species resembles the Greek letter Ω when the niche-constructing intensity differed among species ($\alpha_1 < \alpha_2 < \alpha_3$, Fig. 4b). Different niche-constructing intensities of the three species pushed the extinction of competitive superior: species 2 became extinct when parameter $\gamma > 0$. The most inferior niche constructor (species 1), however, jumped quickly to a higher level of occupancy. The shape of 'Ω' emerged when $\gamma < 0$, particularly in the interval $\gamma \in (-0.15, 0)$ when species occupancies satisfied $P_1 > P_2 > P_3$. Overall, species 1 was the most sensitive one to the difference in extinction rate when niche construction differed among species.

The probability transition model with local dispersal between adjacent patches revealed complicated spatial patterns from the cyclic competition in niche-constructing metapopulations. We selected the arena of 200×200 lattices and presented snapshots of the three species when temporal dynamics of the system reached equilibrium after about 3000 time steps. There were two typical distribution patterns emerged, with the common one of ripples (Fig. 5a) and rare one of rings (Fig. 5b). The spatial pattern changed from tiny ripples to clumped rings with the increase of niche construction intensity. Furthermore, species 1 is always chasing after species 2, species 2 after species 3 and species 3 after species 1. Such local chasing can form riffle-like spatial patterns. The result suggests that niche construction, to a certain degree, constrains the cyclic competition by the feedback between species and their habitat resources. The inter-species differences also have important roles on the spatial patterns of species. The boundary of species distribution, whether their extinction rates were equal or not, became more distinct with gradually increasing inter-species difference δ (shown in Fig. 6). Especially in Fig. 6b, the ring pattern only appeared at low level of inter-species difference ($\delta = 0.05$), and this pattern was very easy to be broken with only a slight increase of inter-species variation. It is worth noting that the spatial pattern does not monotonously depend on parameter δ. Namely, the spatial correlation length decreases but then increases with the increase of δ. Since the correlation length is considered a metric for quantifying spatial synchrony and aggregation [70,71], this result revealed a nonlinear effect of inter-species variation in resource renewing rate on the synchrony of spatial patterns. We suspect that this nonlinear response in spatial synchrony is related to the flipping phenomenon presented in Fig. 3b, where increasing

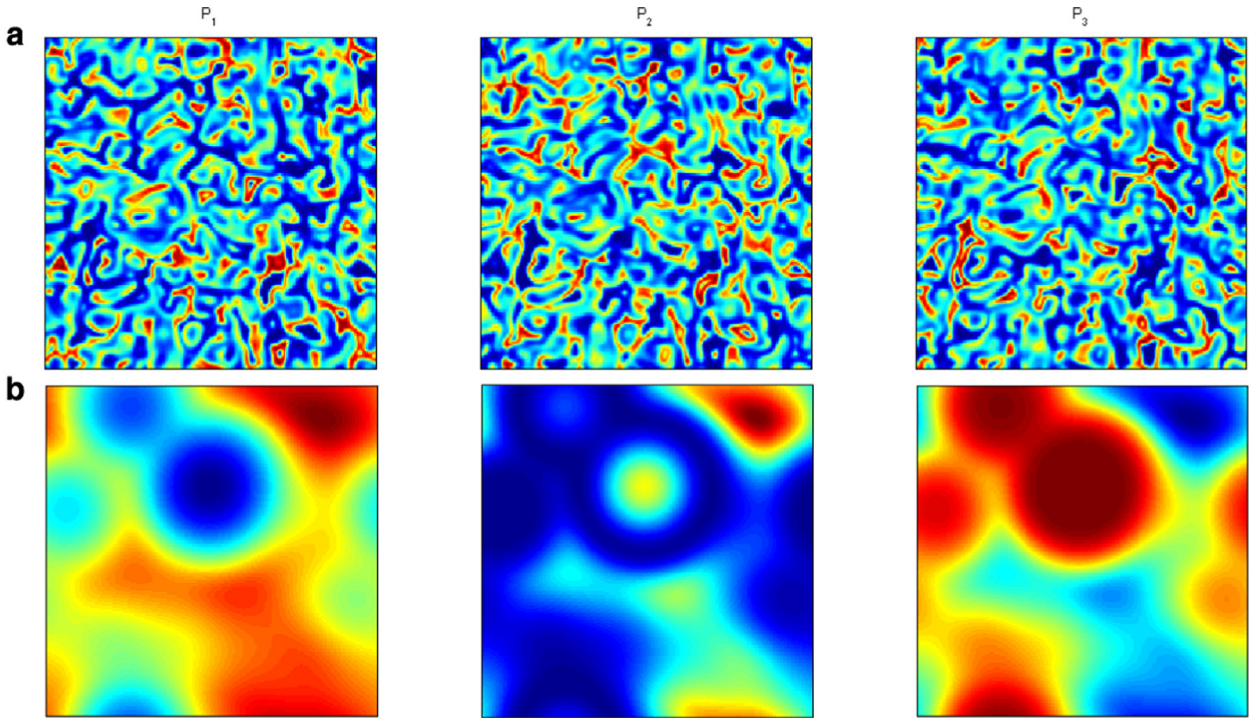

Fig. 5. The spatial patterns of three species with symmetric cyclic competition of niche-constructing metapopulations. The snapshots are at t = 3000. Three species are with identical intensities of niche construction (a) $\alpha_1 = \alpha_2 = \alpha_3 = 0.2$ and (b) $\alpha_1 = \alpha_2 = \alpha_3 = 0.4$, extinction rates are $e_1 = e_2 = e_3 = 0.1$.

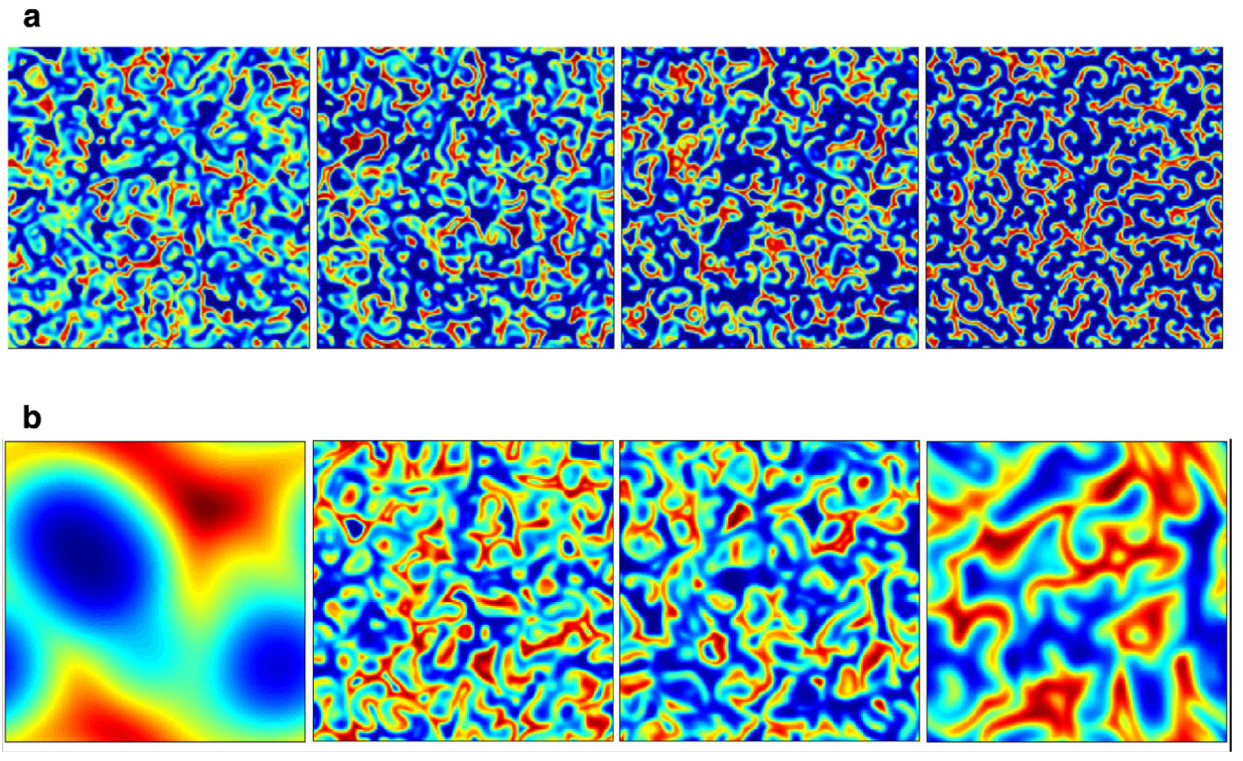

Fig. 6. The spatial patterns of species 2 under asymmetric cyclic competition. The colonization rate of each species satisfies the condition of $c_i = 1 - \alpha_i (i = 1, 2, 3)$. Assume parameter δ describes the interspecies difference, then the three species' abilities of niche construction are $\alpha_1 = \alpha_2 - \delta$, α_2 and $\alpha_3 = \alpha_2 + \delta$. The snapshots are at t = 3000. (a) Parameter δ from left to right respectively is 0.05, 0.1, 0.15 and 0.2. Other parameters are $\alpha_2 = 0.2$ and $e_1 = e_2 = e_3 = 0.1$; (b) parameters δ from left to right are 0.05, 0. 1, 0.2 and 0.3. Other parameters are $\alpha_2 = 0.3$, $e_1 = 0.25$, $e_2 = 0.2$, and $e_3 = 0.15$.

difference in niche-constructing intensities first led to the reduction of occupancy difference but eventually the increase of occupancy difference after two species switched their dominance.

4. Discussion

We have examined the metapopulation model of three niche-constructing species engaging cyclic competition. Through numerical simulations and cellular automata, the system exhibited the dynamics of damped oscillation, periodical fluctuation and stage equilibrium, determined by the intensity of niche construction and extinction rates. In the two-dimensional arena, the three species displayed the spatial patterns of ripples and rings. Diversity in spatial patterns depends on the inter-species differences. The niche construction, which increases their own resource level but reduces the resource of its inferior competitor, plays an important role in system stability and supports species coexistence. Kylafis and Loreau [2] also indicated that niche construction can modify the traditional niche-deteriorating impacts of its agent or its competing species, and thus promotes the potential for species coexistence. Other studies have also supported this conclusion that niche construction can be a key factor for persistence and coexistence in competitive environment [10,15,16,72].

Besides the spatial pattern of ripples, niche construction can also lead to ring-like spatial patterns; this latter one has not been observed in pure cyclically competing metapopulations [58], but was observed in time-lagged niche constructing metapopulations [9]. High intensity of niche construction is likely contributing to the formation of spatial rings. In the metapopulation framework, it has been proved that niche construction is a significant cause of spatial heterogeneity in the environment, through self-regulating feedbacks between organisms and their environment [9,15,72]. The spatial pattern of rings, nevertheless, can be easily disrupted by even small difference in niche construction intensity (Fig. 6b). With the increase of difference among niche-constructing intensities, regardless of the spatial patterns, species distribution became clearly static and fixed in space, distinctively demarcating the boundary of each species. Therefore, niche construction can play the role of a bridge between spatial heterogeneity and biotic interactions to dictate environmental heterogeneity and species' distribution limit [10,15].

The trade-off between the intensity of niche construction and the colonization rate assumed in our model is essential for exploring the system dynamics. Charnov [73] emphasized that the evolutionary theory of life-history allometry in mammals was greatly expanded due to the trade-off between growth rate and life span. For plants, different evolutionary outcomes are possible depending on the shape of trade-off between the rates of niche construction and nutrient uptake ability [2]. Moreover, the trade-off can also decide the ecological consequences of biotic interactions, such as in the classic example on trade-offs between colonization and competition [62,64,74]. Spatial coexistence can arise from the appropriate three-way interspecific trade-offs among competition, colonization and niche construction [15]. In our model, the trade-off between the intensity of niche construction and colonization rate can lead to complex dynamics and spatial patterns. Future works should consider different shapes of trade-off, e.g. convex or concave shape.

The three-species cyclic game is a typical paradigm for exploring the role of population mobility in coexistence, where coexistence can be achieved from a low level of mobility [29]. Different intensities of niche construction in our model means different colonization rates and resource availability of each species, with both affecting the mobility of species. Therefore, our results also emphasize the role of mobility in maintaining diversity in systems of cyclic competition, with the disparity in mobility could threaten species coexistence [26]. Moreover, dispersal and biotic interactions can affect spatial synchrony which increases the extinction risk and undermines metapopulation persistence [75]. Density-dependent dispersal could benefit species persistence through desynchronized dynamics of local populations [76,77]. The self-organized spatial patterns generated here are dependent on mobility of interacting species and can undoubtedly affect spatial synchrony [76,78]. In food webs, the role of mobility on spatial synchrony could cause cascade effect through direct or indirect biotic interactions [79–81]. Here, spatial synchrony is also related to the symmetry breaking. When the three species have identical parameters, increasing niche-constructing intensity can not only transform the system dynamics from disorder to order, but also accelerate the event of extinction of the superior competitor. Once the symmetry is lost, the spatial pattern of rings can be easily disrupted. With increasing disparity between niche-constructing intensities, species distribution became static and fixed in space; that is, niche construction affects both the spatial synchrony and symmetry breaking in cyclic competition.

Extension of the classic cyclic competition from three species (or players) to more have been explored especially in cases modeling microbial communities [82] and large-scale ecological food webs and networks [83–88]. In general, the complexity of spatial pattern and dynamic behavior are drastically increasing with the number of species [27,29,33,34,36]. More investigations are needed for such player-rich cyclical systems, especially on the effects of network topology, mobility and interaction range [30]. Here, niche construction as an important regulating force for local adaptation, established a positive feedback between species and their environments [5,89]. Results from cellular automata have suggested that 'ecological imprint' can emerge through such a reinforcing feedback, forming fine-scale habitat heterogeneity [9,15], thus ensuring biodiversity maintenance via fostering sharp boundaries of species distributions [9,10,15,90]. In any case, n-player cyclic competition games with $n > 3$, together with players affecting each other's niches, deserve further investigation.

Adaptive dynamics, a mathematical approach for studying evolutionary changes, is frequently used to discuss core problems in evolutionary biology, especial polymorphism and diversification through evolutionary branching (e.g. [91–94]). There is much less research about how adaptive divergence between closely related species can affect abiotic environmental conditions and about whether such effects can influence selection pressures so as to either promote or constrain further evolutionary divergence [89,95]. The methodology of adaptive dynamics could hold the key for future breakthrough in studying

the effect of niche construction on evolution because of its concepts and techniques for modeling the dynamics of long-term phenotypic evolution.

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